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Winter Nutrition and Population Ecology of White-Tailed Deer in the Central Superior National Forest

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White-tailed deer (*Odocoileus virginianus*) and wolves (*Canis lupus*) evolved together, and in parts of southern Canada and the northern United States, the two animals still live together. In such areas as northern Minnesota, the wolf is the primary predator on the deer, and the deer is the primary food of the wolf (Stenlund 1955, Mech and Frenzel 1971).

To fully understand the relationship between deer and wolves, it is important to study as many aspects as possible of the life history or ecology of both. Thus, as part of a long-term investigation of wolf-deer interactions in the central Superior National Forest (SNF) of northeastern Minnesota, we have examined deer social ecology, movements, winter nutritional physiology, reproduction, survival, mortality, and population changes.

After some 15 years of such study, we have reached a significant level of understanding of several important features of winter nutrition of deer that relate to the animal's ecology and population dynamics. Thus it is useful at this point to synthesize the existing literature, summarize our findings, and integrate the two.

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DEER FOOD

Deer food studies in the Great Lakes region including the SNF have been reviewed by Rogers *et al.* (1981). Winter food is primarily woody browse, which is low in nutrient quality and digestibility (Ullrey *et al.* 1964, 1967, 1968; Verme and Ullrey 1972; Grigal *et al.* 1979). In contrast, growing-season food includes leaves of non-evergreen terrestrial plants, aquatic plants, mushrooms, and fruits, all more nutritious and digestible than woody browse (Verme and Ullrey 1972). Diet studies in the SNF were primarily based upon feeding site examinations in winter (Wetzel *et al.* 1975, DelGiudice *et al.* 1989b) and summer (Irwin 1974, Hennings 1977). Growing-season diets have been more extensively studied 100 km west of the SNF in similar habitat and are probably representative of diets in the SNF (Kohn and Mooty 1971, Waddell 1973, Mooty 1976).

Winter feeding sites indicated that beaked hazel (*Corylus cornuta*) and mountain maple (*Acer spicatum*) were the primary browse species eaten, followed by red-osier dogwood (*Cornus stolonifera*), round-leaved dogwood (*Cornus rugosa*), red maple (*Acer rubrum*), and Juneberry (*Amelanchier* spp.). In addition to these, at least 44 other taxa were eaten, although in small amounts. Dietary diversity is important to deer nutrition and permits deer to better maintain body weights (Dahlberg and Guettinger 1956, Verme and Ullrey 1972).

Growing-season diets were more diverse than in winter, with a greater number of species occurring more frequently. Predominant taxa included

young aspen (*Populus* spp.), red maple, mountain maple, beaked hazel, bush-honeysuckle (*Diervilla lonicera*), pin cherry (*Prunus pennsylvanica*), choke cherry (*P. virginiana*), bracken fern (*Pteridium aquilinum*), wild sarsaparilla (*Aralia nudicaulis*), aster (*Aster* spp.), and grasses (*Gramineae*).

Feeding site analyses of growing-season diets may be seriously biased from observer error (Rogers *et al.* 1981). Inconspicuous and stemless foods such as mushrooms, berries, nuts, dried leaves, and lichens may be missed entirely, yet could contribute substantially to deer nutrition. Additional work is needed to determine the importance of these food items to northern deer. Furthermore, feeding sites in open areas are easier to find than those in dense forests, so deer living in closed-canopy habitats may be undersampled. Also, deer home range locations are largely determined by social factors (Nelson 1979; Nelson and Mech 1984, 1987), so habitat and food selection at any one site are not a result of a random selective process. Many deer in several locations need to be sampled to obtain a representative sample for a region.

ANNUAL NUTRITIONAL CYCLE

Northern deer experience wide seasonal changes in nutritional status, with the greatest challenge occurring during winter when food quantity and quality are diminished (Short *et al.* 1966, Mautz 1978). Snow may render forage unavailable and impede the mobility, and thus the food intake, of ungulates while also imposing significant energy costs (Verme 1968, Kelsall and Prescott 1971, Moen 1976, Parker *et al.* 1984, Adamczewski *et al.* 1986).

Seasonal variation in the nutrition of northern deer is reflected by annual weight and fat cycles (Mautz 1978, Moen and Severinghaus 1981, Severinghaus 1981). Deer tend to gain weight during late spring and summer, deposit fat in fall, and deplete fat reserves and lose weight as winter progresses into early spring (DelGiudice *et al.* 1990b). Although food quality and accessibility are improved during summer, lactation in does with fawns imposes a nutritional drain from June to late August (Moen 1978). The relative importance to deer survival of autumn repletion of fat reserves versus winter maintenance of body weights has long been of interest to wildlife managers because it is relevant to methods of habitat improvement.

Deer adjust to food scarcity and low ambient temperatures during winter by growing a highly insulative coat, utilizing optimum thermal cover (Ozoga 1968, Verme and Ullrey 1984), and feeding primarily during warmer daylight hours (Ozoga and Verme 1970). They rely heavily upon lipid reserves, and to a lesser extent on body protein, as alternate energy sources, voluntarily restrict their food intake and movements to conserve energy, become "hypothyroid," and experience a decrease in their metabolic rate (French *et al.* 1955, Hoffman and Robinson 1966, Rongstad and Tester 1969, Silver *et al.* 1969, Ozoga and Verme 1970, Seal *et al.* 1972, Bahnak *et al.* 1981). Flexibility in these specializations to changing environments permits deer to survive in a variety of habitats (Slobodkin and Rapoport 1974, Moen 1976, Seal 1978).

However, because ungulates are gravid throughout winter, their annual winter energy deficit can have serious consequences for their offspring, including effects on weight, size, and ultimately survival (Verme 1963, 1977; Mech and Frenzel 1971; Mech and Karns 1977; Rolley and Keith 1980; Thompson 1980; Peterson *et al.* 1982; Adamczewski *et al.* 1986).

PAST STUDIES

The nutritional physiology of white-tailed deer (and Rocky Mountain mule deer, *O. hemionus*) has been more thoroughly studied than that of other wild ungulates. The literature is replete with reports of controlled studies using captive deer to determine dietary energy, protein, and mineral requirements (French *et al.* 1955; Ullrey *et al.* 1970, 1973; Robinette *et al.* 1973; Smith *et al.* 1975; Holter and Hayes 1977) as well as nutritional and seasonal effects on body weight and composition, metabolism (Silver *et al.* 1969; Robbins *et al.* 1974a,b; Moen 1978; Verme and Ozoga 1980; Abbott *et al.* 1984; Torbit *et al.* 1985; Verme 1988), and rumen bacteria and pathology (DeCalesta *et al.* 1974, Hershberger *et al.*

1984). Blood and urine analyses have been utilized increasingly in search of indices of physiological condition in deer (Seal *et al.* 1981; Warren *et al.* 1981, 1982; DelGiudice *et al.* 1987a, 1988b, 1990b).

Additionally, studies have examined the seasonal composition, digestibility, and nutritive value to deer of browse and forage species (Ullrey *et al.* 1964, 1968; Short *et al.* 1966; Robbins and Moen 1975; Blair *et al.* 1980; Pekins and Mautz 1988). Nutritional effects on deer reproductive characteristics have also been scrutinized in captive deer (Murphy and Coates 1966; Verme 1967, 1969; Langenau and Lerg 1976; Ozoga and Verme 1982).

Nutritional condition of free-ranging deer has been examined in relation to season, range condition, sex, and age via the effects of these factors on body weights, fat reserves, and other morphological measurements, and blood and urine profiles (Harris 1945; Rosen and Bischoff 1952; Hoffman and Robinson 1966; Seal and Erickson 1969; Anderson *et al.* 1972; Coblentz 1975; Seal *et al.* 1978; Moen and Severinghaus 1981; Severinghaus 1981; Kie *et al.* 1983; Waid and Warren 1984; Cothran *et al.* 1987; DelGiudice *et al.* 1989a,b, 1990a).

DEER STUDIES IN THE SNF

Study Area

Our study area lies within the central Superior National Forest, northeastern Minnesota, 48° N, 92° W. (fig. 1). The area is characterized by a series of low rocky ridges, infertile soil, and numerous lakes and waterways. During winter, mean daily minimum and maximum temperatures range from -20° and -9.6° C in January to -1.8° and 9.9° C in April. Ambient temperatures below 17.8° C (0° F) generally occur on 51 days during winter (National Oceanic and Atmosphere Administration 1985). Winters of northeastern Minnesota are characterized by mean snowfalls of 150 cm from November through April and snow depths up to 110 cm (Nelson and Mech 1981).

Mixed coniferous-deciduous stands are prominent on the uplands and include balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), paper birch (*Betula papyrifera*), trembling aspen (*P. tremuloides*), jack pine (*Pinus banksiana*), and northern white-cedar (*Thuja occidentalis*). Beaked hazel and speckled alder (*Alnus rugosa*) are dominant shrubs on the site (Wetzel *et al.* 1975). Conifer swamps are populated by black

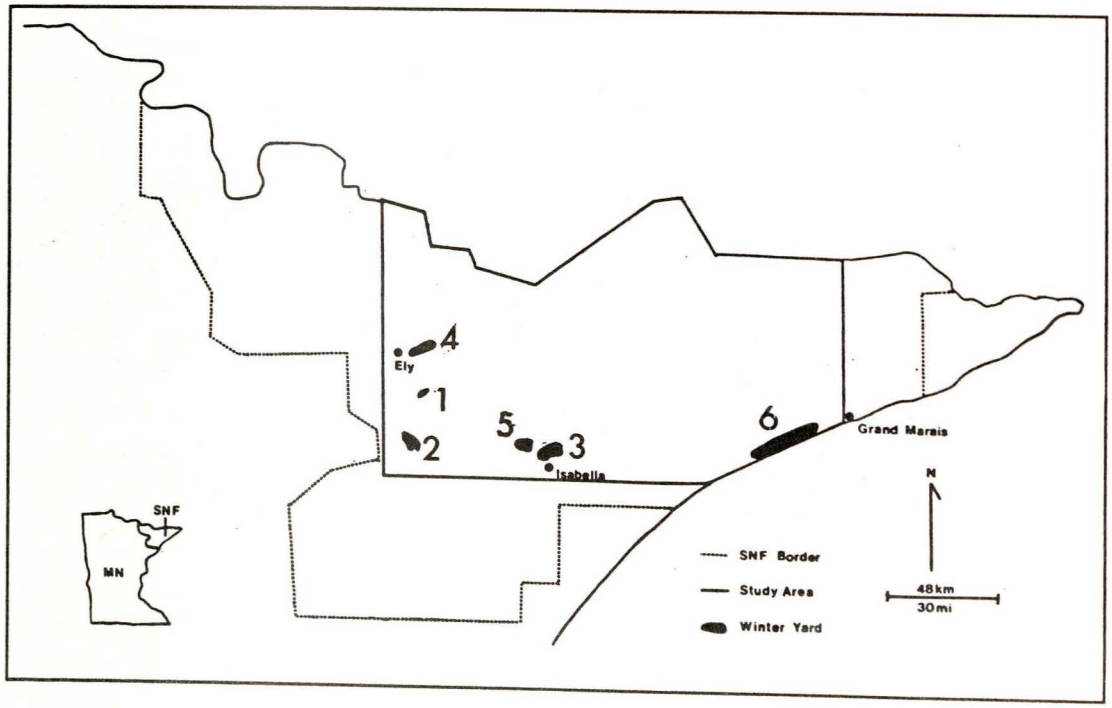

Figure 1.—*The Superior National Forest study area including winter yards: (1) Kawishiwi, (2) Snort Lake, (3) Isabella, (4) Garden Lake, (5) Bushel Lake, and (6) Jonvick.*

spruce (*Picea mariana*), tamarack (*Larix laricina*), northern white-cedar, bog birch (*Betula pumila*), and Labrador tea (*Ledum groenlandicum*). Logging of hardwoods has occurred on the study site for pulp production and to enhance deer habitat quality (T. R. Biebighauser[1], personal communication).

Much of our work has focused on three subpopulations of deer that winter in the Kawishiwi (KAW) (50 deer), Isabella (ISA) (400 deer), and Snort Lake (SL) (50 deer) yards, covering 7, 27, and 6 km^2, respectively. Adult deer from these winter yards use different, largely exclusive, summer ranges (Nelson and Mech 1987). Isabella is notably different from the other deer yards in elevation and winter severity index (WSI) (DelGiudice *et al.* 1989a). Mean elevation is 457 m at KAW and SL and 549 m at ISA. Mean maximum snow cover is generally 30 percent deeper at ISA (Minnesota Department of Natural Resources, unpublished data) and melts later; during March snow depth may be two times deeper at ISA than at KAW and SL (DelGiudice *et al.* 1989a). These differences have facilitated natural comparisons of the effects of snow depth on the physiological status of deer during winter (DelGiudice *et al.* 1989a).

Three additional yards were also studied but less intensively—the Bushel Lake near Isabella, and the Garden Lake near Ely and Jonvick on the north shore of Lake Superior, both with snow regimes and temperatures similar to those at KAW (Nelson and Mech 1981).

CAPTIVE DEER STUDIES

In addition to the field investigation, we also resorted to nutritional studies of captive deer (DelGiudice *et al.* 1987a,b, 1988b, 1990b). Such controlled studies of the effects of nutritional variations on captive deer physiology are essential to identifying useful indices of nutritional status that may be applied to free-ranging deer. Because all deer lie somewhere along a nutritional continuum, findings generated from captive deer are also critical to an accurate interpretation of data collected from free-ranging deer existing under less known environmental conditions.

Basic requirements of optimal nutritional indices are that they be: sensitive to subtle changes in nutrition, useful in assessing a deer's body condition and chances of survival, and easily obtainable. Our controlled studies simultaneously examined the effects of various degrees of nutritional decline during winter and recovery during early spring on numerous blood and urinary characteristics and on body weights and composition. Additionally, we investigated the feasibility of collecting and chemically analyzing urine in snow (snow-urine) for metabolites identified as useful nutritional indices.

RESULTS

Following is a summary of results from pertinent studies that characterize much of the social-ecology and winter nutritional physiology of the central SNF deer population.

Deer Home Ranges, Yarding, and Migrations

Weather, habitat, and wolf predation are the primary factors influencing seasonal home ranges, yarding behavior, and migrations of deer in the SNF (Hoskinson and Mech 1976; Nelson 1979; Nelson and Mech 1981, 1984, 1987). Nutrition is most likely the critical mechanism of interaction amongst these factors.

Adult does occupy summer and fall ranges of 83 $\pm$ 9 (SE) and 147 $\pm$ 59 ha, respectively; winter ranges (18 $\pm$ 2) are greatly reduced (Nelson and Mech 1981). After fawning, does with fawns are widely dispersed and occupy smaller ranges (38 $\pm$ 8 ha), possibly to reduce feeding competition, conserve energy reserves during lactation, and minimize exposure to predation (Moen 1976, Nelson and Mech 1981). Smaller fall ranges of adult does compared to adult males (749 $\pm$ 226) may be related to the need of does for nutritional recovery after lactation.

Deer exhibit a high degree of fidelity for winter yards, and decreases in ambient temperature appear to be most influential in inducing fall migration to their yards (Verme 1973, Hoskinson and Mech 1976, Nelson and Mech 1981). Individual deer migrate at varying times; thus they

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may have different physiological thresholds to thermal changes that induce migration, and these thresholds may be related to nutritional status. Deer nutritional status is critically related to snow depth because movement in snow cover ≥ 40 cm deep is energetically costly (Mattfeld 1974, Moen 1976, Parker *et al.* 1984).

Movement by deer within yards is greatly reduced by February (Nelson and Mech 1981, 1987) and is associated with diminished food intake, thyroid activity, and metabolic rates (Silver *et al.* 1969, Ozoga and Verme 1970, Seal *et al.* 1972). This appears to be an integrated behavioral and physiological response to food scarcity that facilitates energy conservation.

Winter yarding by deer seems to have two primary advantages related to their nutrition and survival. Well-used trail systems permit access to forage and escape from wolves, and groups of deer have an increased ability to detect predators, which allows individuals to spend more time eating and ruminating (Nelson and Mech 1981). There are also thermal benefits of conifer cover, and increased use of such cover has been correlated with increased snow depth and density (Ozoga 1968). However, in the yards, diets are less diverse, and beaked hazel becomes a major food item (Wetzel *et al.* 1975, DelGiudice *et al.* 1989b).

Spring migration generally occurs in late March and early April and also appears to be related to changes in temperature and subsequent snowmelt. Delays in warm temperatures (5-10° C) after snowmelt began, even when snow depth was <20 cm, have been associated with prolonged residence by deer in winter yards (Nelson and Mech 1981). However, increased metabolic rates and depleted fat reserves may lower physiological thresholds of deer for temperature increases inducing earlier migration.

Deer Population Trends

From the early 1900's to the late 1960's, white-tailed deer inhabited most of the SNF (Olson 1938, Stenlund 1955, Mech and Karns 1977). Winter deer densities approximated 5 deer/km² from 1953 through 1968-1969 (Nelson and Mech 1986a); high fawn:doe ratios (≥85:100) were documented from 1955 until winter 1964. However, from winter 1968-1969 through 1977-1978, the population declined by 80 to 90 percent (fig. 2), attributable to wolf predation and maturing forests but driven by severe winters (Mech and Frenzel 1971, Mech and Karns 1977, Nelson and Mech 1986a). Deer were decimated in the east-central portion of the SNF interior during winter. By 1970-1971, the wolf population began a steady decrease as well (fig. 2) (Mech 1986). The deer decline was followed by a period of stability, then a general increase from winter 1983-1984 until the present (fig. 2).

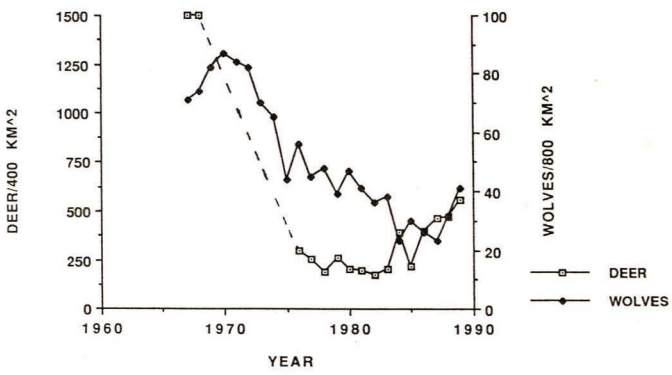

Figure 2.—*White-tailed deer and wolf population trends in the central Superior National Forest, Minnesota, during winter, 1968-1989 (compiled from Mech 1986, unpublished data; Nelson and Mech 1986a).*

Evidence strongly suggests an inverse relationship between winter severity and population size. All but two winters during the 1955-1964 interval of high fawn:doe ratios were considered mild. However, several years of decreasing fawn:doe ratios associated with severe winters preceded the population decline that began in 1968-1969 (Mech and Karns 1977). Except for 3 years, the SNF continued to experience severe winters every year from 1968-1969 to 1977-1978 (table 1, Nelson and Mech 1981). The winter severity index, based on snow depth and density and heat loss to the environment, has long been used

as a measure of winter's impact on deer. A WSI >100-125 is considered detrimental to deer in Minnesota (Verme 1968; P. D. Karns[2], personal communication); the WSI averaged 151 throughout the 10-year deer decline.

Nelson and Mech (1986b,c) found diminished monthly survival rates in deer during winter. Wolf predation was the primary mortality factor, but there was no relationship between number of wolves and predation rate; instead predation on deer was directly related ($R^2 = 0.51$, $P < 0.02$) to snow depth. Fawns were most vulnerable. In a study of the effects of snow depth and density on forage availability and quality, Adamczewski *et al.* (1986) associated high calf mortality in caribou (*Rangifer tarandus*) with prolonged deep snow.

Besides the direct effect of snow depth on ungulate vulnerability, there are also indirect effects through prenatal nutrition. Severe winter weather can adversely influence fetal development and reduce neonatal survival (Verme 1977). Weight and survival of deer fawns born later in spring, and autumn fawn:doe ratios have been inversely related to increased snow depth (Verme 1963, 1977; Mech and Karns 1977). Similar observations have been documented for moose (*Alces alces*) (Rolley and Keith 1980, Thompson 1980, Peterson *et al.* 1982).

Data collected from 1958-1985 showed inverse relationships between multi-winter snow accumulations and fawn:doe ratios and population size for deer in the SNF and moose twinning rates and calf:cow ratios on Isle Royale (Mech *et al.* 1987). Thus it is clear that snow depth, by hindering foraging by deer, affects their nutritional condition and ultimately their survival and the survival of their offspring.

Physiological Indicators of Nutrition

Because the causal chain between wolf predation on deer and predisposing influences of the environment has led us most recently to investigations into deer physiology and nutrition, we detail below our pertinent attempts to find metabolic indices of a deer's condition, just what these indices indicate, and the relationship of condition to environment.

As in humans and other mammals, blood and urinary constituents in deer may be used as metabolic indicators to determine the severity of nutritional deprivation. For such indicators to be interpreted accurately in free-ranging deer, the effects of changes in nutritional intake on animal condition (*e.g.*, endogenous protein and fat reserves) and their collective influence on "reference values" of these indicators must first be established (Seal *et al.* 1981).

We have conducted three nutritional studies of captive deer; thus far, reference values generated from two of these studies (DelGiudice *et al.* 1987a,b, 1990b) have facilitated data interpretation for nutritional assessments of free-ranging deer in the SNF.

In studying the simultaneous effects of chronic winter undernutrition on body weight and composition (determined *in vivo* with tritiated water) and on blood and urinary characteristics of captive white-tailed deer (December 18, 1984 to May 3, 1985), we confirmed that deer voluntarily reduce their feed consumption until late March (Week 10, fig. 3) (DelGiudice *et al.* 1990b). As previously mentioned, such changes in dietary intake have been observed elsewhere and have also been associated with decreases in metabolic rates (Silver *et al.* 1969).

Although our deer increased their intake during late March, they continued to lose weight through early April (Week 12, fig. 3) because of the poor quality of their diet. Subsequent refeeding of a high protein-high energy diet to simulate spring-greenup feeding (fig. 3) appeared to be essential to initiating a nutritional recovery, indicated by further increases in food consumption accompanied by weight gain (DelGiudice *et al.* 1990b). Similarly, we have observed deer that were completely nutritionally deprived for a prolonged period compensate by consuming more high quality food when refed than control animals less severely undernuourished (DelGiudice *et al.* 1987a).

Percent body protein loss is directly related ($R^2 = 0.91$) to percent weight loss (fig. 4) in deer (DelGiudice *et al.* 1990b) and other mammals, and the 12.8 ± 2.0 percent peak weight loss we

[2]*Mailing address: Minnesota Department of Natural Resources, St. Paul, MN 55101.*

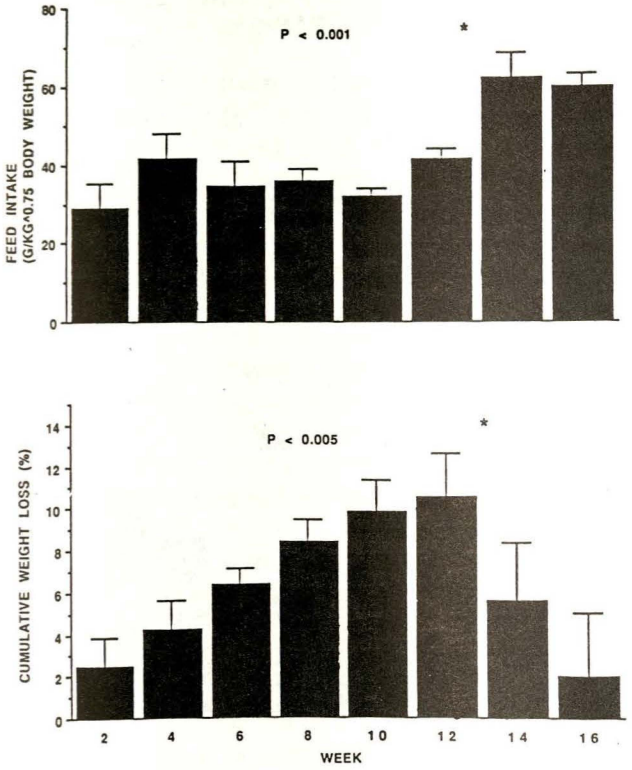

Figure 3.—*Mean (+ SE) feed intake and cumulative weight loss per 2-week interval in six captive adult white-tailed deer, Grand Rapids, Minnesota, January 10-May 3, 1985. Deer were nutritionally restricted from after handling on Week 0 until Week 12, then refed a high protein-high energy diet (DelGiudice* et al. *1990b).*

observed in our undernourished deer from December 18 to early April was accompanied by an estimated 12.5 percent protein loss. However, this was considered a classic "protein-sparing" rate of catabolism that occurs during early phases of undernutrition (Torbit *et al.* 1985) as the deer relied primarily on their fat reserves for energy; fat reserves were depleted by a minimum of 85 percent. Although exact figures are not possible, this would translate into a far greater absolute weight of fat lost compared to body protein.

Generally, mammals cannot tolerate protein losses much greater than 33 percent (Cahill

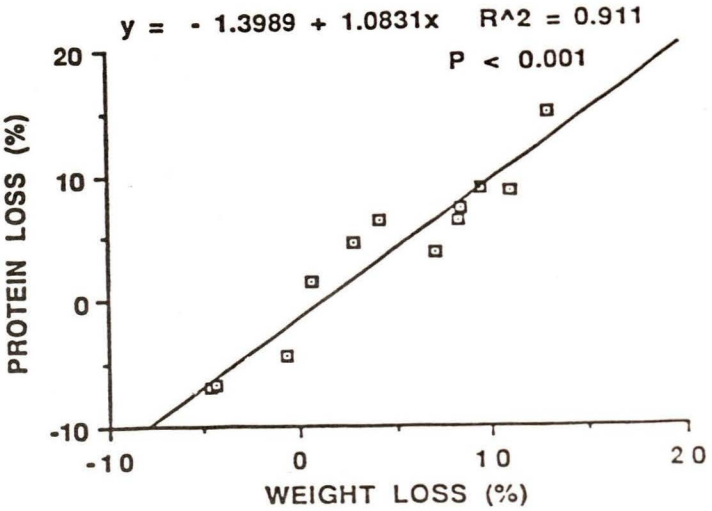

Figure 4.—*Relationship between endogenous protein loss and weight loss in six captive adult white-tailed deer, Grand Rapids, Minnesota, January 24-April 17, 1985 (DelGiudice* et al. *1990b).*

1970), although this depends somewhat on baseline nutritional status and body composition. The rate of protein catabolism, and thus the degree of protein-sparing, depends upon repleteness of fat reserves and the magnitude of dietary energy and protein deficits (Forbes 1985, Torbit *et al.* 1985). Extreme undernutrition, starvation, and exhausted fat reserves are associated with accelerated net protein catabolism (DelGiudice *et al.* 1987a,b, 1990b). Undernutrition and complete nutritional deprivation in deer are also accompanied by dehydration (DelGiudice *et al.* 1987a, 1990b).

Several blood and urine characteristics are useful for monitoring the nutritional condition of deer. Elevated hemoglobin (Hb) concentrations, red blood cell (RBC) counts, and/or packed cell volumes (PCV's), indicative of hemoconcentration attributable to dehydration, have been noted in our fasted and chronically undernourished deer (DelGiudice *et al.* 1987a, 1990b). Decreases in these characteristics occurred within 2 weeks of refeeding these deer high quality diets and reflected increased hydration states and initiation of nutritional recovery (DelGiudice *et al.* 1987a, 1990b).

Urea is the end product of protein (dietary and endogenous) metabolism, and serum urea nitrogen (SUN) is linearly related to dietary crude protein intake in deer (Robbins *et al.* 1974b), as long as dietary energy is adequate and body protein is being spared (DelGiudice *et al.* 1987a, 1990b; DelGiudice and Seal 1988). In our chronically undernourished captive deer, progressively decreasing mean SUN concentrations until Week 12 (10.1 ± 2.0 mg/dl) (fig. 5) reflected the decrease in protein intake, the sparing of body protein, the recycling of UN (Robbins *et al.* 1974b, DelGiudice *et al.* 1990b), and the persistence of fat reserves (Robbins *et al.* 1974b, DelGiudice and Seal 1988, DelGiudice *et al.* 1990b). Increases in intake of the high quality feed during the recovery were indicated by increases in SUN (DelGiudice *et al.* 1990b).

In contrast, fasted deer had elevated mean SUN concentrations (>30 mg/dl) comparable to or greater than values in control deer receiving diets with 7 to 13 percent crude protein; these values in the latter were indicative of accelerated protein catabolism and more extreme nutritional deprivation (DelGiudice *et al.* 1987a). These deer lost at least 17.5 ± 3.9 percent of their peak winter weight, but probably more because the study did not begin until late February (DelGiudice *et al.* 1987a). Upon refeeding, SUN values in these deer decreased from the high catabolic levels they exhibited during fasting.

Chronic undernutrition of our deer was also evidenced by decreases in thyroxine (T_4) (fig. 5), which is related to the diminished energy intake (Seal *et al.* 1972). Similarly, decreased T_4 concentrations occurred in our fasted deer (DelGiudice *et al.* 1987a). Four weeks of nutritional recovery were indicated by elevated T_4 values in the previously undernourished (fig. 5) and fasted deer (DelGiudice *et al.* 1987a, 1990b).

Urinary excretion of urea nitrogen, often expressed as urea nitrogen:creatinine (U:C) ratios, showed patterns similar to those of SUN in our chronically undernourished deer (fig. 5) and fasted deer (DelGiudice *et al.* 1987a, 1990b). DelGiudice and Seal (1988) presented a classification system of three phases of winter undernutrition in northern deer—early, prolonged-reversible, and prolonged-irreversible—based on SUN and urinary U:C ratios.

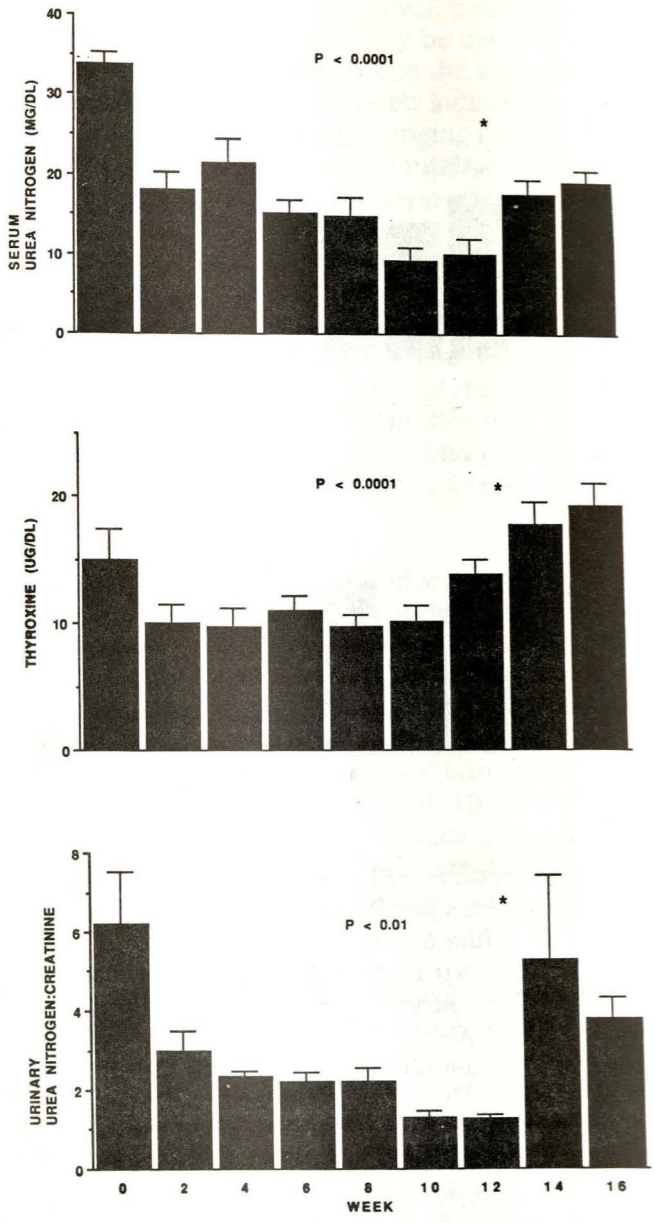

Figure 5.—*Mean (+ SE) values for serum urea nitrogen, thyroxine, and urinary urea nitrogen:creatinine ratios in six captive, adult white-tailed deer, Grand Rapids, Minnesota, January 10-May 3, 1985. Deer were nutritionally restricted from after handling on Week 0 until Week 12, then refed a high protein-high energy diet (DelGiudice* et al. *1990b).*

Assessing the Herd by Blood and by Snow-Urine

We collected blood from 40 free-ranging deer inhabiting four winter yards in 1974 and 1975 (Seal *et al.* 1978). Eight blood characteristics exhibited differences among the populations related to habitat or location effects. Of special interest, deer from the yard with the most mature and coniferous habitat (Bushel Lake) had the lowest dietary protein and energy intake as indicated by SUN, RBC counts, non-esterified fatty acids, and T_4 levels (table 1). Deer from three other yards displayed better nutritional intake that was related to younger and more deciduous habitat, one yard being the KAW also examined by DelGiudice *et al.* (1989a).

Urinalysis may be a more sensitive means of assessing the physiological status of deer (DelGiudice *et al.* 1987b, 1988b; DelGiudice and Seal 1988) than blood analyses, and chemical analysis of urine excreted in snow (snow-urine) is an accurate, efficient means of collecting physiological data from northern free-ranging deer during winter (DelGiudice *et al.* 1988a, 1989a). Snow-urine samples may be collected up to 5 or more days after excretion and stored frozen without altering of creatinine ratios of metabolites (DelGiudice *et al.* 1988a). We found no difference in U:C, sodium:creatinine (Na:C), and potassium:creatinine (K:C) ratios in snow-urine samples compared to bladder urines from which they were produced (DelGiudice *et al.* 1988a); U:C (fig. 6), Na:C, and K:C were directly related in corresponding bladder urine and respective snow-urine samples (G. D. DelGiudice, University of Minnesota, Department of Fisheries & Wildlife, unpublished data).

We sequentially collected and chemically analyzed snow-urine for U, Na, K, calcium (Ca), and phosphorous (P) in a comparison of the physiological status of free-ranging deer in the KAW, SL, ISA, and SF winter yards from January 1 to

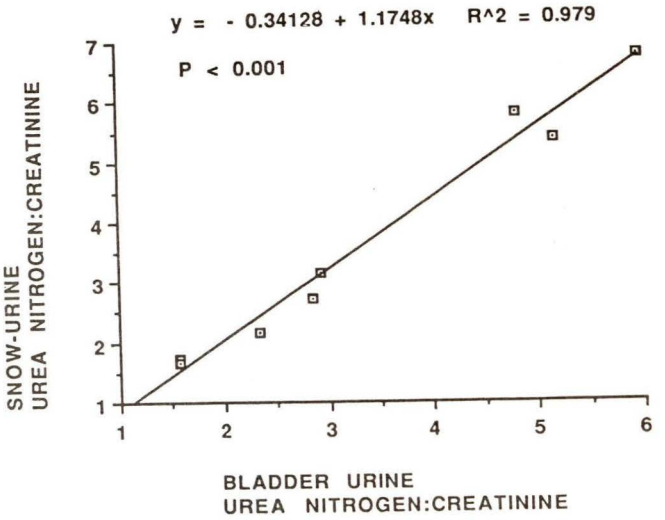

Figure 6.—*Relationship between urea nitrogen:creatinine ratios in bladder urine and those urine samples deposited in snow (snow-urine) (compiled from DelGiudice* et al. *1988a).*

Table 1.—*Differences (P < 0.05) in blood characteristics among white-tailed deer residing in four winter yards, northeastern Minnesota, winter 1974-1975 (from Seal* et al. *1978)*

Blood characteristics[1]	Winter yards							
	Jonvick		Bushel Lake		Kawishiwi		Garden Lake	
	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE	$\bar{X}$	SE
RBC (10^6/ul)	11.0	0.8	9.2	0.3	12.4	0.9	11.5	0.4
SUN (mg/dl)	16.0	1.4	8.4	1.3	10.4	1.6	15.2	2.2
T_4 (ug/dl)	9.2	1.1	6.6	0.4	12.9	1.5	9.1	1.4
NEFA (uEq/L)	540	102	656	144	829	89	237	30

[1]RBC = red blood cells, SUN = serum urea nitrogen, T_4 = thyroxine, and NEFA = non-esterified fatty acids.

March 31, 1985 (DelGiudice *et al.* 1989a). Deer in the ISA-SF yard were supplementally fed a commercial diet and served as nutritional controls. Declining trends of U:C, (fig. 7), Na:C, and K:C in the KAW and ISA deer indicated increasingly inadequate nutrition as winter progressed. However, absence of U:C ratios indicative of prolonged undernutrition indicated that these deer were not catabolizing body protein at an accelerated rate and thus had not depleted their fat reserves and were probably receiving adequate dietary energy (DelGiudice *et al.* 1987a, 1990b; DelGiudice and Seal 1988). Unaltered values of these ratios (U:C, fig. 7) and P:C in snow-urine collected at SL reflected stable levels of nutrient availability. Browse availability and use by deer at SL were more diverse than at KAW until late winter and throughout winter compared to ISA (DelGiudice *et al.* 1989b).

Significant ($P < 0.05$) elevations of Na:C, K:C, and P:C at KAW and SL suggested initiation of nutritional recovery in deer during late March; snow cover was ≤18 cm in both yards (DelGiudice *et al.* 1989a). In contrast, deep snow (36 cm) at ISA continued to restrict feeding and limit dietary diversity of deer and was associated with electrolyte ratios that remained diminished. Greater U:C (fig. 7), Na:C, and K:C at ISA-SF provided physiological evidence of the higher nutritional status of supplementally fed deer throughout winter and their ability to increase nutrient intake during late March despite prolonged deep snow. Frequent and quantitative assessments of the physiological status of deer by snow-urine analysis helped us better understand the relationship between snow cover and the nutritional well-being of deer.

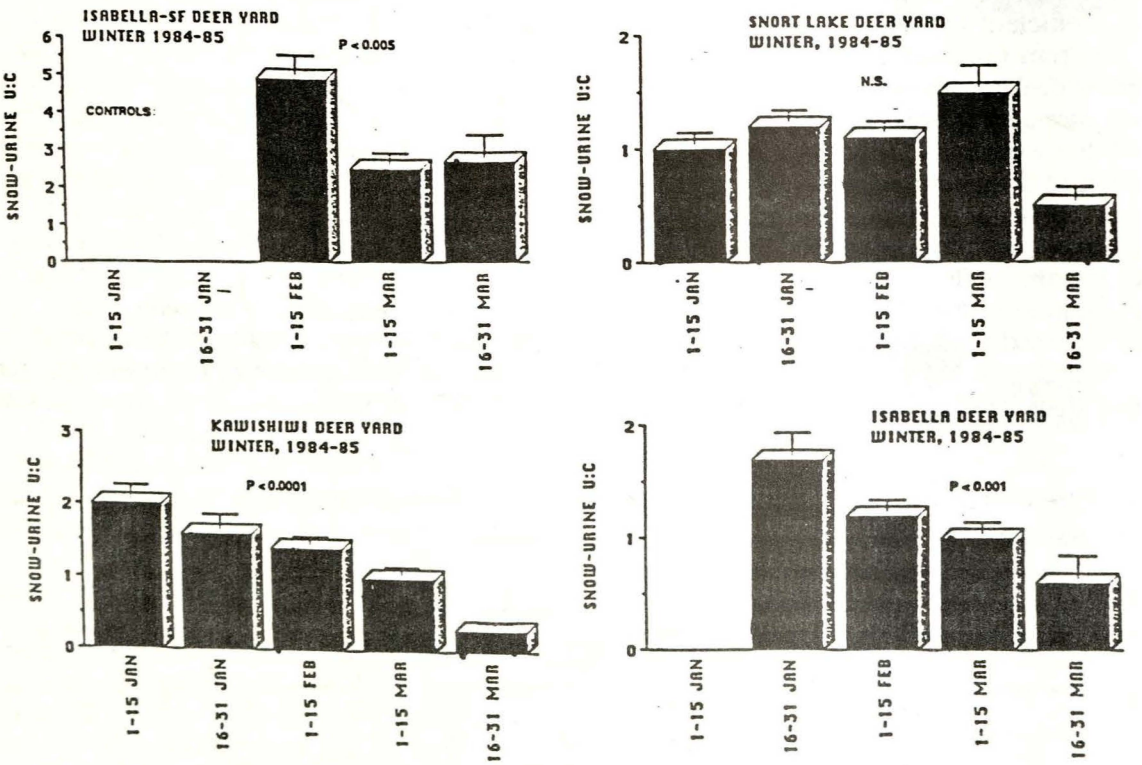

Figure 7.—*Mean (+ SE) urea nitrogen:creatinine (U:C) in white-tailed deer urine in snow (snow-urine) collected during 2-week intervals in the Isabella-SF, Kawishiwi, Snort Lake, and Isabella winter yards, northeastern Minnesota, 1985 (compiled from* DelGiudice et al. *1989a).*

SUMMARY AND CONCLUSIONS

Changes in SNF deer numbers over time are modulated by several environmental factors including food supply, which is a function of habitat; weather conditions, which affect the ability of deer to reach food; and wolf predation, which takes advantage of any weaknesses in individual deer resulting from the other factors. Although wolf predation is the most obvious direct cause of deer mortality, a thorough understanding of deer population trends requires a close look at underlying basic influences on the life of the deer.

Nutrition is one of the most basic factors affecting any animal. As a result of the studies and findings described above, the methodology is now available to assess the nutritional condition of individual deer via blood and urine samples, and of deer populations via sampling of urine in snow. This will allow more refined investigations into the highly complex relationships among habitat, winter weather, deer condition, and wolf predation.

Meanwhile, it is clear that as the combination of habitat conditions and winter weather turns favorable, the deer herd responds by increasing. Wolves still prey on vulnerable deer, but such individuals make up a small percent of the herd, and wolves have little effect in slowing deer population growth. Conversely, when food and winter weather deteriorate, proportionately more deer become vulnerable. Wolves take advantage of such an increased food supply and help drive the population lower.

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Summarizes 15 years of studying white-tailed deer social ecology, movements, winter nutritional physiology, reproduction, survival, mortality, and population changes in the central Superior National Forest. Applies results of nutritional experiments with captive deer to interpretation of data from wild deer.

KEY WORDS: Deer, ecology, nutrition, wolves, predation.

Our job at the North Central Forest Experiment Station is discovering and creating new knowledge and technology in the field of natural resources and conveying this information to the people who can use it. As a new generation of forests emerges in our region, managers are confronted with two unique challenges: (1) Dealing with the great diversity in composition, quality, and ownership of the forests, and (2) Reconciling the conflicting demands of the people who use them. Helping the forest manager meet these challenges while protecting the environment is what research at North Central is all about.

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